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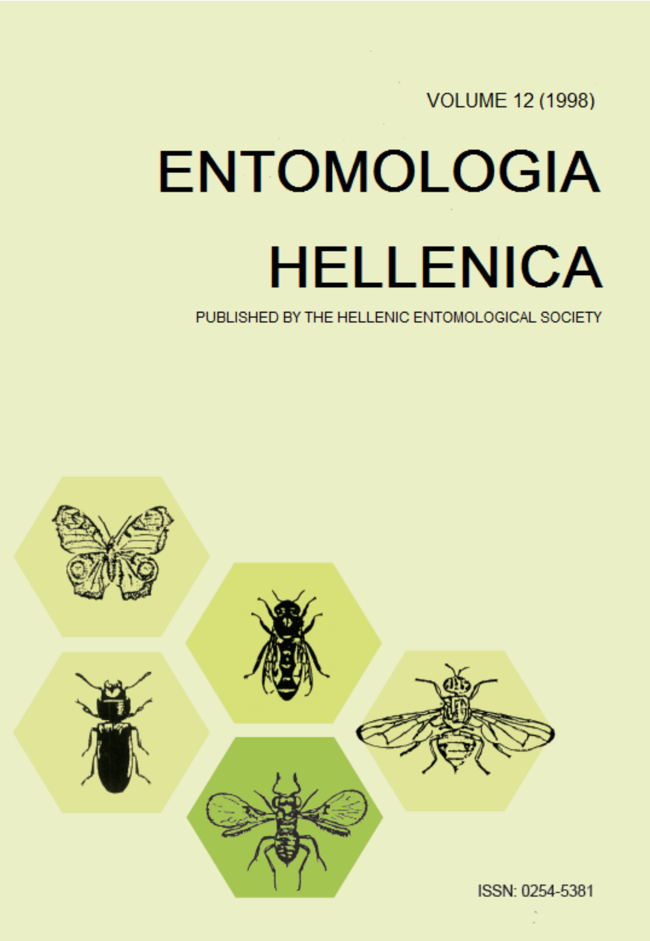

Geographic Variation of Diapause Induction and Termination in the Spider Mite Tetranychus urticae: A mini-review

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Geographic Variation of Diapause Induction and Termination in the Spider Mite *Tetranychus urticae*: A mini-review[1]

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ABSTRACT

In eight strains of the spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae), originating from different localities in Europe, the critical daylength for diapause induction and termination was almost the same in each strain but varied with the latitudinal origin of the strains; critical daylength was shorter in strains originating from lower latitudes and longer in those from higher latitudes. Diapause intensity, measured as the period of chilling required for diapause termination under a short day photoperiod (LD 10:14) and 19°C, again varied with the latitudinal origin of each strain, being higher the more northern the origin of the strain. An exception were two mountain strains which showed a longer critical daylength and a deeper diapause than expected on the basis of their latitudinal origin. The number of long-day (LD 17:7) cycles required for 50% diapause termination after a certain period of chilling was higher in the northern and lower in the southern strains. These results indicate that geographic strains of *T. urticae* may differ considerably in their diapause attributes, which may be explained as an adaptation to local climatic conditions. The great plasticity of the diapause response may, among other factors, have been responsible for the wide distribution of this mite species.

Among insects and mites, diapause is the most widespread type of dormancy, which enables them to survive seasons unfavourable for development and reproduction and to synchronize their life cycles with the changing of the seasons (e.g. Beck, 1980; Tauber et al., 1986; Danks 1987).

In the spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae), diapause occurs in adult females only, and is induced by short-day photoperiods experienced during the immature stages. Diapause termination is also under the control of photoperiod. In a Dutch strain of *T. urticae*, under a long-day photoperiod diapause is terminated rapidly after a period of about 2 weeks of chilling at 4° C, whereas under a short-day photoperiod diapause is not terminated even after 2.5 months of chilling (Veerman, 1977; 1985).

In insect and mite species with widespread distribution, diapause characteristics may vary in relation to latitude, altitude and local climatic conditions. This geographic variation may concern characteristics such as the critical photoperiod for diapause induction as well as diapause intensity, and may be seen as an adaptive mechanism to dif-

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ferent local environmental conditions (Masaki, 1961; Danilevskii, 1965; Tauber et al., 1986; Danks, 1987). Geographic variation in the critical daylength for diapause induction has been found in different strains of *T. urticae* from the former USSR (Bondarenko and Khay-Yuan (1958), in strains from Japan (Gotoh and Shinkaji, 1981; Takafuji, 1994) and in strains from Europe (Vaz Nunes et al., 1990). In all these cases, the critical daylength was closely related to latitude, being shorter in the southern and longer in the northern strains. Diapause development in *T. urticae* is favoured by low temperatures (Bondarenko 1958; Parr and Hussey, 1966; Veerman, 1977). Differences in the period of chilling required for diapause termination in different strains of *T. urticae* may indicate differences in diapause intensity, as found for populations of *T. urticae* from nearby areas in England (Parr and Hussey, 1966). In certain insect species a correlation has been found between diapause intensity and the geographic origin of the strain, diapause intensity being higher in the more northern strains (Krysan and Branson, 1977; Sims, 1982).

In the present paper, a short review is given of our work on geographic variation of diapause characteristics in eight strains of *T. urticae* from Europe. We studied whether there is a relationship between the geographic origin of each strain and diapause characteristics such as the critical daylength for diapause induction and termination, the diapause duration and the number of long-day cycles required for diapause termination. The ecological significance of the geographic variation of these diapause attributes is discussed.

Geographic variation in the critical daylength for diapause induction and termination

The strains of *T. urticae* originated from different localities in Europe, as shown in Table 1. Details concerning rearing and maintenance of the experimental mites are given by Koveos (1995). The photoperiodic response curves for diapause induction and termination in eight strains of *T. urticae* from different latitudes in Europe are shown in Figure 1. In all these strains, daylengths

TABLE 1. Origin of geographic strains of *Tetramychus urticae* used by Koveos et al (1993b).

Strain	Origin	Collector	Original hostplant	Date	Latitude (°N)	Altitude (m)
L	Leningrad, USSR	Dr. K.F. Geispitz, Entomological Laboratory Leningrad State University	*Aegopodium podagraria*	1975	60	—
W	Warwaw, Poland	Dr M. Vaz Numes, Laboratory of Experimental Entomology, University of Amsterdam	*Cucumis sativus*	1985	52.5	—
V	Voorne, The Netherlands	Prof. W. Helle, Laboratory of Experimental Entolomogy, Univeristy of Amsterdam	*Sambucus nigra*	1961	52	—
S_I	Susch, Untergadun,	Mr. H.R. Bolland, Laboratory of Experimental Entomology, University of Amsterdam	*Polygonatum verticillatum*	1984	47	1450
P	Padua, Italy	Dr. P. Ivancich Gambaro, Institute of Agricultural Entomoloty, University of Padua	*Prunus persica*	1986	45.5	—
A	Ailefroide, Massif des Ecrins, France	Mr. H.R. Bolland, Laboratory of Experimental Engomology University of Amsterdam	*Rubus idaeus*	1986	45	1515
T_I	Thessaloniki, Greece	Dr. N. Koulousis, Laboratory of Applied Zoology and Parasitology University of Thessaloniki	*Cucumis sativus*	1988	40.5	—
T_{II}	Thessaloniki, Greece	Dr. D. Stavridis, Laboratory of Applied Zoology and Parasitology University of Thessaloniki	*Phaseolus vulgaris*	1988	40.5	—

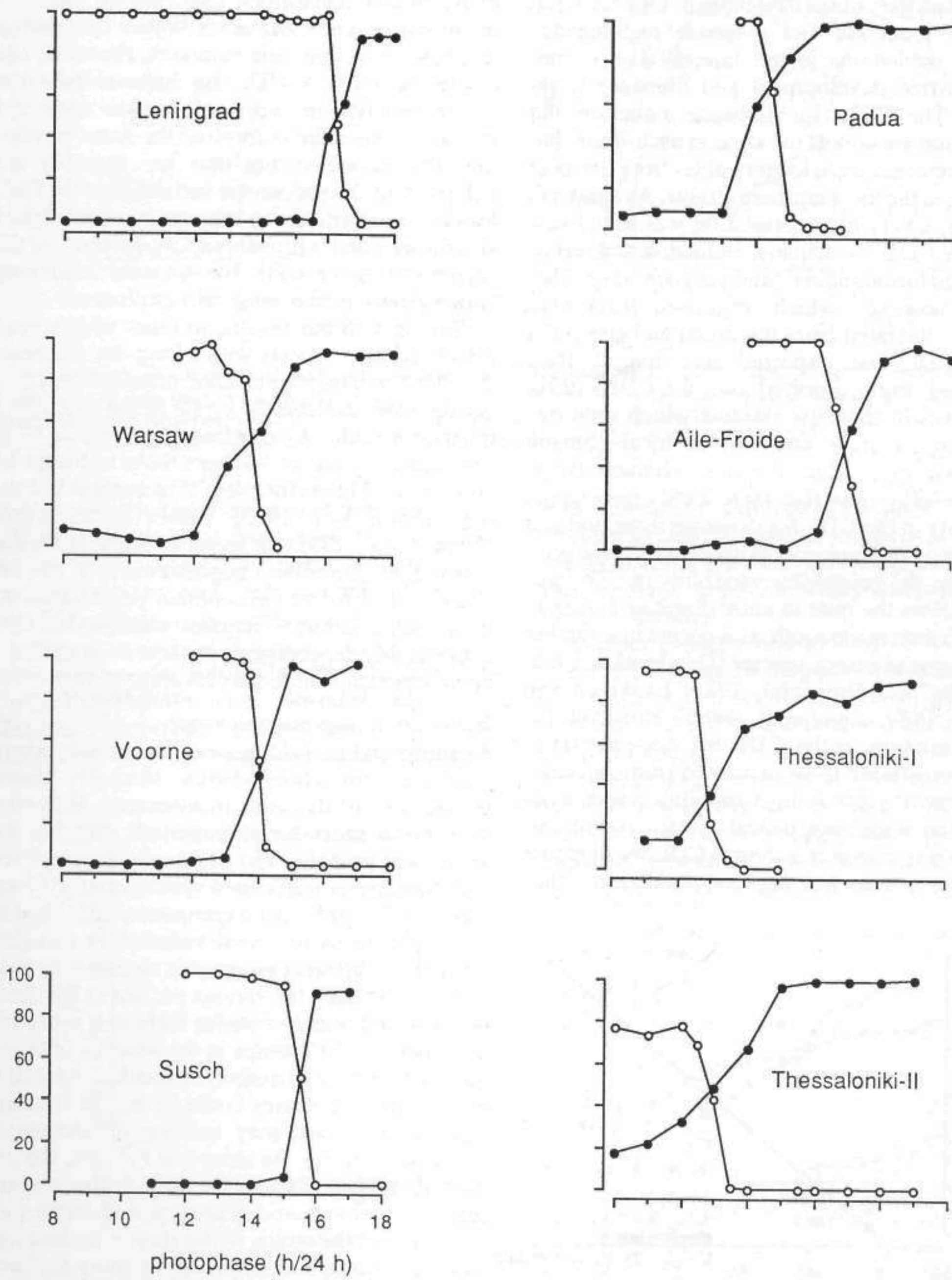

FIG. 1. Photoperiodic response curves for diapause induction (open symbols) and diapause termination (filled symbols) in eight strains of *Tetranychus urticae* from different latitudes and altitudes in Europe (see Table 1). In diapause termination experiments, the diapause females were kept at 4° C for certain days before being transferred to the series of photoperiods and 19° C. The duration of cold storage was 11 days for Thessaloniki-I and Thessaloniki-II; 21 days for Padua, Warsaw, Voorne and Leningrad; 28 days for Ailefroide and 42 days for Susch. Percentages of diapause termination were determined after 10 days for Thessaloniki-I, Thessaloniki-II, Padua, Warsaw and Leningrad; after 14 days for Voorne and Ailefroide; and after 20 days for Susch (data from Koveos et al., 1993a, with permission of SAGE Science Press).

shorter than the critical daylength (CDL) favoured diapause induction and diapause maintenance whereas daylengths longer than CDL favoured diapause-free development and diapause termination. The CDLs for diapause induction and termination are almost the same in each strain, but shift systematically to longer values from the most southern to the most northern strains. As shown in Figure 2, a very high correlation was found between the CDL for diapause induction and termination and the latitudinal origin of each strain. Two strains, however, which originated from high altitudes, deviated from this trend and showed a longer CDL than expected according to their latitudinal origin. Furthermore, the CDLs differ even between these two strains which indicates that except latitude and altitude local climatic conditions may affect diapause characteristics. These results show that there exists geographic variability in the CDL for diapause induction and termination in *T. urticae*. With regard to diapause induction, the geographic variability in CDL probably allows the mite to enter diapause earlier in the north than in the south, as it occurs in a number of widespread insect species (Danilevskii, 1965; Bradshaw and Holzapfel, 1983; Lankinen and Lumme, 1984; Sauer et al., 1986). However, the clinal variation in the CDL for diapause termination is difficult to be explained from an ecological point of view. If this variability is seen as an adaptation of the mite to local climatic conditions, then we might expect a shorter CDL for diapause termination than for diapause induction, since

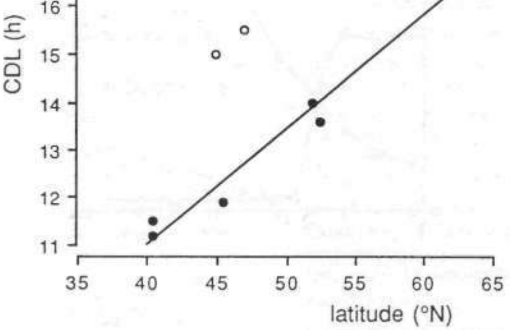

FIG. 2. Latitudinal cline in critical daylength for diapause termination in six lowland strains of *Tetranychus urticae* (filled symbols). (y=0.25x+1.09; r=0.962). The open symbols represent the two mountain strains (cf. Table 1) (data from Koveos et al., 1993a, with permission of SAGE Science Press).

under natural conditions CDL during diapause maintenance (early winter) is shorter than during diapause induction (late summer). However, our results show that the CDLs for diapause induction and termination in each strain are the same and probably under the control of the same physiological mechanism and thus are probably not independent. Therefore, the variability of the CDL for diapause termination may not be of ecological significance and is probably a "by-product" of the variability in the CDL for diapause induction, which clearly is of ecological significance.

Similarly to our results, in other wide-spread insect and mite species with a long-day response, the CDL for diapause induction often becomes longer the more nothern the origin of the strain. In a number of such long-day insect species, the CDL for diapause induction has been found to change by about 1 to 1.5 hours for every 5° increase in latitude (e.g. Danilevskii, 1965; Tauber et al., 1986; Nechols et al., 1987). In Japan, diapause incidence was higher in northern populations of *T. urticae* and very low to zero in southern populations. At intermediate latitudes diapause was found to vary considerably depending on the host plant and local environmental conditions (Takafuji, 1994).

Variation in diapause intensity

As shown in Fig. 1, long-day photoperiods favour diapause termination whereas short-day photoperiods favour diapause maintenance. However, even under short-day photoperiods diapause development proceeds and eventually is completed and diapause is terminated spontaneously (Veerman, 1977; 1985). An experimental tool used in our experiments to reveal variation in diapause intensity in different geographic strains, is to keep diapause females for various periods at low temperature and then to transfer them to a short-day photoperiod. Differences in the period of chilling required for 50% diapause termination in females of the different strains could be due to intrinsic characteristics and may indicate differences in diapause intensity. As shown in Fig. 3A, the period of chilling required for 50% diapause termination under a short-day photoperiod varies with the origin of the strain, being shorter in the more southern strains and longer in the more northern strains. In the most southern strain from Greece diapause was terminated in 50% of the females after a period of only about 20 days at 4° C, whereas in the most northern strain from Leningrad about 60 days at 4° C were required. Under the long-day photoperiod, diapause was terminated rapidly and much earlier than under the short-

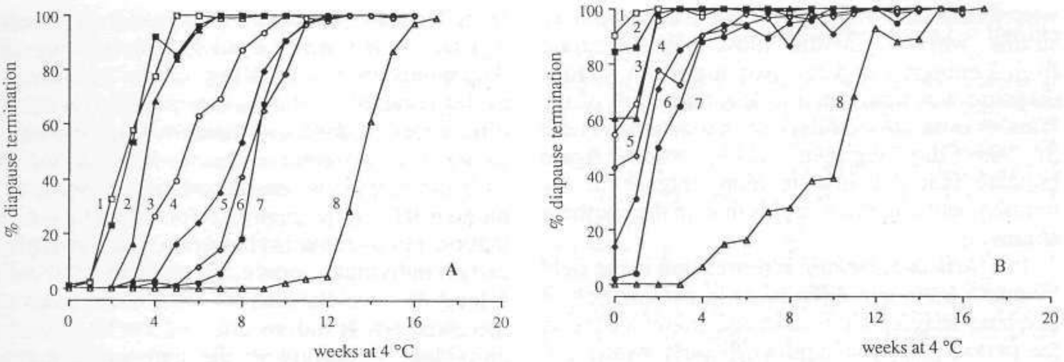

FIG. 3. Effect of photoperiod and duration of cold exposure on diapause termination in eight strains of *Tetranychus urticae* from different localities in Europe. Diapausing females were kept for a varying period of time at 4° C before being transferred to (A) short days (LD 10:14) or (B) long days (LD 17:7). Curves (1) TI; (2) TII; (3)P; (4)V; (5)W; (6)A; (7)L; (8)SI (cf. Table 1) (data from Koveos et al., 1993b, with permission of Blackwell Science Ltd.).

day photoperiod and in the southern strain from Thessaloniki even without any cold storage. As shown in Fig. 4, the more northern the origin of the strain the longer the period of chilling required for 50% diapause termination and therefore the higher the intensity of diapause. However, the two strains from the mountains deviate from this trend; they require a longer period of chilling than expected according to their latitudinal origin. Moreover, although these two strains originated from very similar latitudes and altitudes, they differ considerably in diapause intensity. It is, therefore, concluded that, except latitude and altitude, local climatic conditions may seriously affect diapause duration.

Another experimental tool which we used to reveal differences in diapause intensity, was to keep diapause females of the different strains for a certain period at 4° C and then to transfer them to LD 10:14 and 19° C. Under this short-day photoperiod diapause is terminated spontaneously and therefore any differences in the period of maintenance in these conditions resulting in 50% diapause termination may indicate differences in diapause intensity. As shown in Fig. 5, diapause

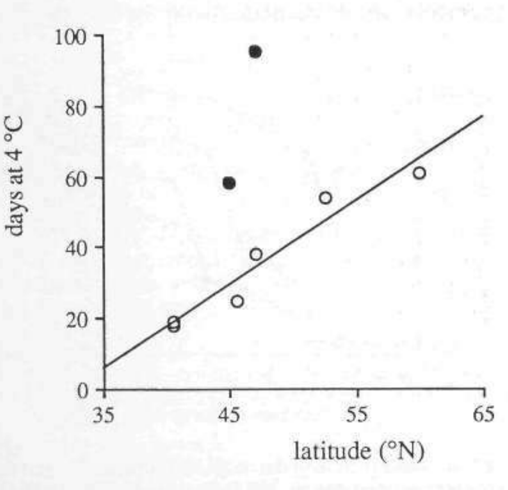

FIG. 4. Latitudinal cline in the period of chilling at 4° C required for 50% diapause termination under a short day photoperiod (LD 10:14) at 19° C, to which the mites were transferred after cold storage, in six lowland strains of *Tetranychus urticae* (open symbols) (y=2.36x+77.66; r=0.936). The closed symbols represent the two mountain strains. (cf. Table 1) (data from Koveos et al., 1993b, with permission of Science Blackwell Ltd).

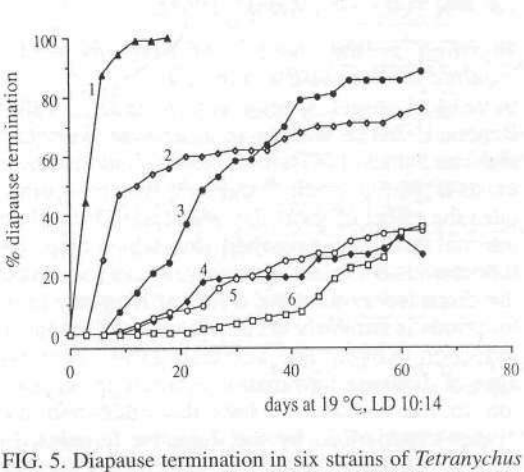

FIG. 5. Diapause termination in six strains of *Tetranychus urticae* under short days (LD 10:14) at 19° C, after 5 weeks of cold exposure (4° C). (1) TI; (2) P; (3) V; (4) A; (5) L; (6) SI (cf. Table 1) (data from Koveos et al., 1993b, with permission of Science Blackwell Ltd.).

was terminated rapidly in the most southern strains whereas in the most nothern strain from Leningrad and the two mountain strains, diapause was terminated in less than 35% of the females even after 60 days of maintenance under the short-day regimen. These results again indicate that diapause is more intense in the northern and mountain strains than in the southern strains.

In *T. urticae*, diapause is terminated in the field by mid-winter, and differences in the duration of diapause may concern diapause maintenance in the period from late summer to early winter (cf. Veerman, 1985). Another consequence of the clinal variation in the duration of diapause is that in northern populations the number of generations per year is lower than in the southern ones (Masaki, 1984). In certain insect species as the rice stem borer *Chilo suppressalis,* the emma field cricket *Gryllulus migratus* and the gypsy moth *Lymantria dispar* the duration of diapause is shorter in the northern than in the southern populations (Masaki, 1961), whereas in some others as the cricket *Pteronemobius fascipes* (Masaki, 1961) and the moth *Acronycta rumicis* (Danilevskii, 1965) the opposite was found to be true. These reverse trends in diapause duration between different geographic populations may be explained with reference to voltinism, i.e. if a species has a constant voltinism in different areas of its geographic distribution then it would be expected that diapause duration may be longer in the southern than in the northern populations, whereas the opposite may be true in species with variable voltinism (Masaki, 1961).

Variation in the number of long-day cycles required for diapause termination

In several insect species (cf. Saunders, 1982; Beach, 1978) as well as in *T. urticae* (Veerman and Vaz Nunes, 1987), it has been found that there exists a photoperiodic "counter", which accumulates the effect of short-day photoperiods until an internal threshold is reached after which diapause induction is complete. Recently, it was found that the diapause-terminating effect of long-day photoperiods is similarly accumulated as in diapause induction (Koveos and Veerman, 1994). Percentages of diapause termination increase in proportion to the number of long-day photoperiodic cycles experienced by the diapause females. In three geographic strains of *T. urticae* the number of long-day photoperiodic cycles required for 50% diapause termination varied with the latitudinal origin of the strain. It was 2-3 in the strain from Thessaloniki, 5-6 in the strain from Voorne and 6-7 in the strain from Leningrad (Fig. 6). Apparently, this variability in the number of cycles required for diapause termination is due to differences in diapause intensity characteristics between the different strains. In addition, within each strain, there is considerable variability in the number of cycles required for diapause termination. For example, in the strain from Leningrad certain individuals terminated diapause after only 4 long-day cycles, whereas other individuals of the same strain did so after 12 cycles. Similar individual variability in the number of cycles required for diapause induction was found in earlier experiments with *T. urticae* (Veerman and Vaz Nunes, 1987).

The geographic variability in diapause induction and termination characteristics of *T. urticae* shows the importance of diapause as an adaptive mechanism for survival in different geographic areas. In addition, it may explain to some extent differences in voltinism and phenology in various geographic strains of this mite species. Furthermore, this mite species, because of its wide geographic distribution and the two sharp responses to photoperiod (induction and termination of diapause) has been used extensively for analysing the physiological mechanism controlling photoperiodic induction. Using different experimental protocols, and in particular with the help of reso-

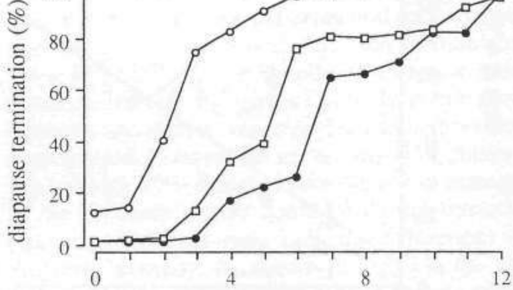

FIG. 6. Number of long day (LD 17:7) cycles required for diapause termination at 19° C in three strains of *Tetranychus urticae* after a cold exposure of 2 weeks at 4° C. After experiencing the indicating number of short-night cycles the mites were transferred to continuous darkness at 19° C. Percentages of diapause temination were determined 12 days after removal from cold storage. Closed circles: Leningrad; open squares Voorne; open circles: Thessaloniki-II (cf. Table 1) (data from Koveos and Veerman, 1994, with permission of Elsevier Science Ltd.)

nance experiments, it has been shown that an hourglass-like mechanism controls both induction and termination of diapause in all the geographic strains studied of this mite species, and that the circadian system probably exerts a modifying effect which is revealed only in unnaturally extended nights (Veerman and Koveos, 1989; Veerman and Koveos, 1991; Vaz Nunes et al., 1990; Koveos et al., 1993a,b; Veerman, 1994; Koveos and Veerman, 1994). These results may help answering one of the main questions in the field of photoperiodism, viz. the question concerning the unity or diversity of the physiological mechanism controlling photoperiodic induction, in insects and mites (cf. Veerman, 1994).

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KEY WORDS: Photoperiodism, Geographic variation, Diapause, Spider mites, *Tetranychus urticae*

Γεωγραφική Παραλλακτικότητα στην Πρόκληση και Περάτωση της Διάπαυσης του Ακάρεως *Tetranychus urticae*

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ΠΕΡΙΛΗΨΗ

Σε οκτώ φυλές του ακάρεως *Tetranychus urticae* Koch (Acari: Tetranychidae) που προέρχονταν από διαφορετικές περιοχές της Ευρώπης, η κρίσιμη φωτόφαση για την πρόκληση και περάτωση της διάπαυσης ήταν σχεδόν η ίδια σε κάθε φυλή, αλλά διέφερε ανάλογα με τη γεωγραφική προέλευση της φυλής. Η κρίσιμη φωτόφαση είχε μικρότερη διάρκεια σε φυλές που προέρχονταν από μικρά γεωγραφικά πλάτη και μεγαλύτερη διάρκεια σε φυλές από μεγάλα γεωγραφικά πλάτη. Η ένταση της διάπαυσης, μετρούμενη ως η απαιτούμενη περίοδος έκθεσης των διαπαυόντων ατόμων σε χαμηλές θερμοκρασίες για την περάτωση της διάπαυσης, διέφερε επίσης και ήταν μεγαλύτερη όσο μεγαλύτερο ήταν το γεωγραφικό πλάτος προέλευσης της φυλής. Κατ' εξαίρεση δύο φυλές που προέρχονταν από ορεινές περιοχές, είχαν μεγαλύτερη τιμή κρίσιμης φωτόφασης και μεγαλύτερη ένταση διάπαυσης από ότι αναμενόταν με βάση το γεωγραφικό πλάτος προέλευσής τους. Ο αριθμός των φωτοπεριοδικών κύκλων με μεγάλη διάρκεια φωτόφασης που απαιτούνταν για την περάτωση της διάπαυσης στο 50% των ατόμων μετά από ορισμένη περίοδο ψύξης, ήταν μεγαλύτερος στις βόρειες και μικρότερος στις νότιες φυλές. Τα αποτελέσματα αυτά δείχνουν ότι γεωγραφικές φυλές του *T. urticae* μπορεί να διαφέρουν σε αξιόλογο βαθμό ως προς τα χαρακτηριστικά της διάπαυσης, κάτι που προφανώς αποτελεί μηχανισμό προσαρμογής σε τοπικές κλιματικές συνθήκες. Η μεγάλη πλαστικότητα των χαρακτηριστικών της διάπαυσης μπορεί, μεταξύ άλλων παραγόντων, να είναι υπεύθυνη για την ευρεία γεωγραφική διάδοση του είδους αυτού.